UNDERSTANDING THE NUMBERS AND DISTRIBUTION OF WADERS AND OTHER ANIMALS IN A CHANGING WORLD: *HABITAT CHOICE* AS THE LOCK AND THE KEY*

THEUNIS PIERSMA

Animal Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, P.O. Box 45, 9750 AA Haren, The Netherlands.
Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

On 19 October 2004 Koos van Zomeren finished his series of public lectures[1] as writer in residence at the University of Groningen with the following sentence: *"- in the animal all characteristics of the landscape come together, in the landscape all characteristics of the animal are spread out*." Here I like to start with this beautiful line, or rather, with the first part of the sentence: "*in the animal all characteristics of the landscape come together*."

With these words Van Zomeren gives a powerful summary of that which makes most animal ecologists tick. He also suggests why animal ecology, in addition to the beauty and elegance of the science itself, could be relevant in a societal context.

Animal ecologists try to understand the habitat choice of animals, they investigate the place and role of animals within a landscape, within sets of interconnected landscapes, within certain habitats in certain climate zones, in the world. Animal ecologists try to discover the mechanisms underlying the distribution and abundance of animals.[2] The *urgency* of our science comes from the increasingly human driven changes in this world and the increasing speed of these changes: the rapidity with which landscapes are altered.

Let me begin by identifying some of mechanisms that help us explain habitat choice and the distribution and abundance of animals in changing worlds. What does an animal ecologist think of when confronted with a distributional problem or a change in numbers? What are the keys to explain an animal's distribution, and why is it locked in this state? What would she or he try to measure?

An animal that doesn't eat will starve and die: food is a first condition for survival. With information on the distribution of food, lots can be said about the behaviour of animals that eat that food, and sometimes about their numbers. Thus, we must know what an animal eats, and how prey are distributed over the range of that animal. Building on a 50 year long tradition of Dutch mudflat studies,[3] we have since 1988 investigated the distribution and abundance of Red Knots *Calidris canutus* in the Wadden Sea. We chose knots as a model migrant shorebird in view of their uniform diet of molluscs, a diet that can quite easily be quantified by visual observation and faecal analyses.[4] We also chose Knots because of their strict habitat choice. Non-breeding knots only occur on extensive intertidal flats.[5] With the ships and moveable observation platforms of the Royal Netherlands Institute for Sea Research on Texel such intertidal flats are accessible to us. We have managed to determine the distribution of molluscs over hundreds of square kilometres of intertidal flats for many years.[6]

We have also managed to follow individual Red Knots throughout day and night by applying one and a half gram radio transmitters to their backs and registering their absence or presence within a certain radius with automated radio tracking stations (ARTS). In this way we came to grips with the tidal and daily movements of individual Red Knots. The birds that roosted at Richel during high tide periods, in the course of several days, appeared to use the whole complex of intertidal flats between the island of Vlieland and the Friesian foreshore.[7]

By mapping benthic food availability over much of this area of intertidal flats, we also built a detailed picture of the distribution of their food. In this map (Figure 1), the size of the black dots scales with the predicted average food intake rate at each of these sampling stations: the blacker the area, the more food there is for Red Knots to find.

Most Red Knots use that great sandbank, Richel, to roost. With the outgoing tide they have to decide whether to fly to forage on the intertidal flats of Westwad, or Richelwad, or Grienderwaard or Ballastplaat. *They* have to ask themselves whether it is worth travelling all the way to the Ballastplaat, twenty kilometres from Richel, or whether the poorer intertidal flats closer to Richel are good enough. *We* have to ask ourselves whether Red Knots have all the relevant information to take such strategic decisions.

Figure 2 shows the way that Red Knots with radio tags that roost at Richel distribute themselves at low tide.[8] Many birds remained close to the high tide roost, many birds moved to the Grienderwaard, but the rich mudflats of the Ballastplaat appeared not particularly popular. Apparently many Red Knots decided against the long commute to Ballastplaat: perhaps flight costs prevent this being worth their while.

To evaluate the decisions made by Red Knots we can compare the empirical distribution pattern with predicted distribution patterns, predictions made on the basis of models that either do or do not incorporate their omniscience and travel costs.[8] Red Knots that do not know the distribution of their food, and do not care about the travel costs of reaching the various places, should distribute themselves across the different areas relative to the extents of these areas (Figure 1). Under these assumptions many Red

* *Editor's note. This essay is based on the text of the author's Inaugural Lecture as Professor in Animal Ecology presented at the University of Groningen on 21 February 2005. The full text of the address is available from the author.*

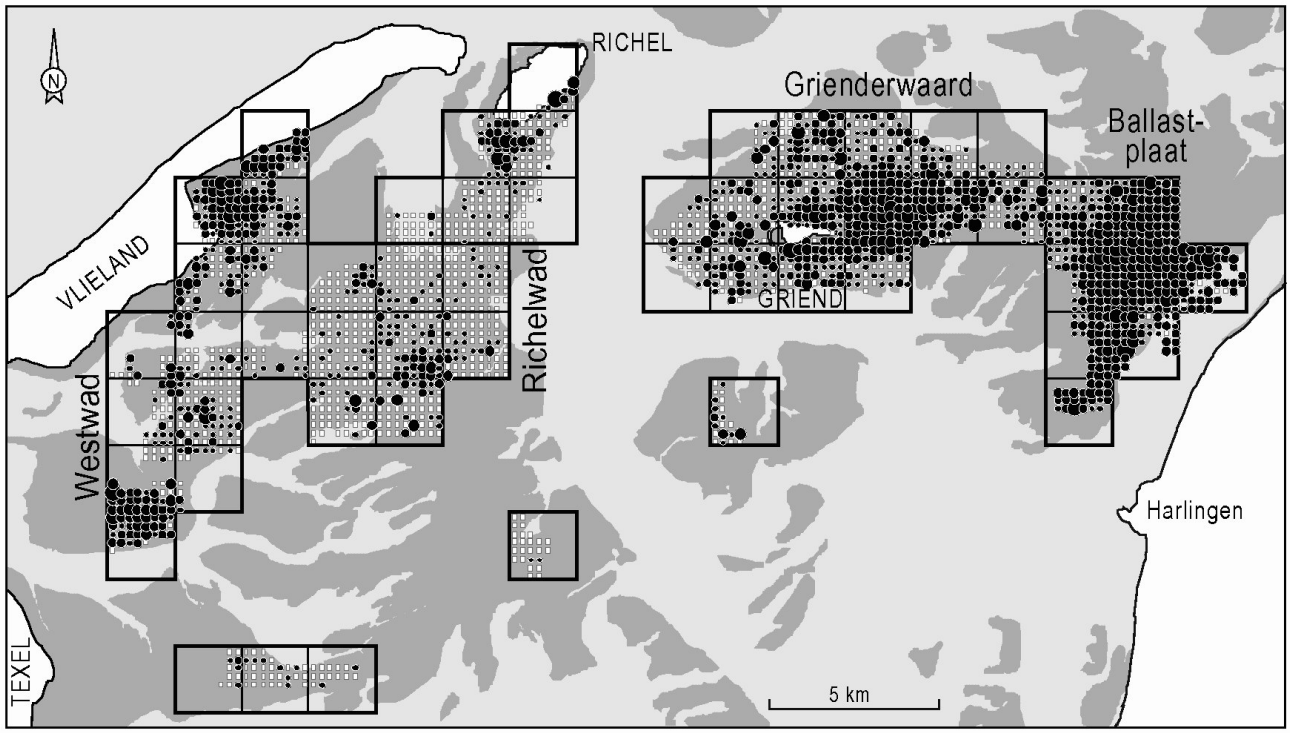

Figure 1. Map of the mudflats in the western Dutch Wadden Sea, with an outline of the annual benthic sampling grid with 250 meter intersections. White dots indicate sites where Red Knots would not have found anything to eat in August-September 1996-2000. The size of the black dots is scaled to the predicted intake rate averaged across the five years of study (August-September 1996-2000). This map is based on van Gils *et al*. (2006).[8]

Knots should go to the large flats of Westwad, for example. Red Knots that lack the information on food distribution but do take travel costs into account should remain close to Richel even at low tide. Red Knots that know as much about the distribution of their food as we do, but that don't account for travel costs, should travel to Ballastplaat in much larger numbers than we saw. Finally, omniscient Red Knots that take travel costs into account should distribute themselves approximately according to the real, wild knots. In the words of the scientist their behaviour is consistent with the assumption that they know the distribution of their food really well and that they incorporate flight costs into their strategic decisions. In the words of the writer (van Zomeren), in [*the behaviour of*] the animal all [*relevant*] characteristics of the landscape come together.

Red Knots, and animals in general, have to balance their energy income and energy expenditure, that is, animals have to do ENERGY MANAGEMENT. In areas where daytime air temperatures exceed body temperatures, about forty-one degrees Celsius in the case of birds, animals can only prevent overheating by finding cool shaded locations or by using body water for evaporative cooling.[9] Especially under such conditions the maintenance of energy balance is closely coupled with the maintenance of a water balance (WATER MANAGEMENT).[10]

Over the last thirty years, the animal ecologists from the University of Groningen, under the keen leadership of Rudi Drent, have built up a certain reputation with their detailed mechanistic analyses of the distribution and numbers of especially waterbirds.[11] The distribution models are built on thorough measurements of food availability and detailed empirical knowledge on energy expenditure and water balance. Yet, the maintenance of an energy and a water balance are only two of the considerations that animals should routinely take into account. Birds that fall victim to predators such as a Peregrine Falcon *Falco peregrinus*, for example, won't have as many descendants as birds who avoid the attentions of this dangerous beast. The inescapability of evolutionary mechanisms then ensures that animals do also take danger into account. That is, animals have to find the right balance between fear and external danger; they have to do DANGER MANAGEMENT'.[12]

This leads me to the second part of Van Zomeren's deep statement: that *in the landscape all characteristics of the animal are spread out*. This line troubled me, as most landscapes harbour many different animals. How on earth can their characteristics be spread out in that landscape? Nevertheless, the logic began to make some sense when I started thinking about my own considerations about birds that breed in the extreme High Arctic in summer and all move to marine and saline habitats in winter. If there are reasons to think that in harsh and extreme polar climates parasites and pathogens are rare, there are also reasons to think that the chicks of tundra-breeding birds may not get a chance to build up proper immune systems. They would then have to restrict themselves to relatively 'clean' (i.e. parasite and pathogen poor) habitats during the rest of their lives. Marine, seaside and otherwise saline habitats may provide such clean areas.[13]

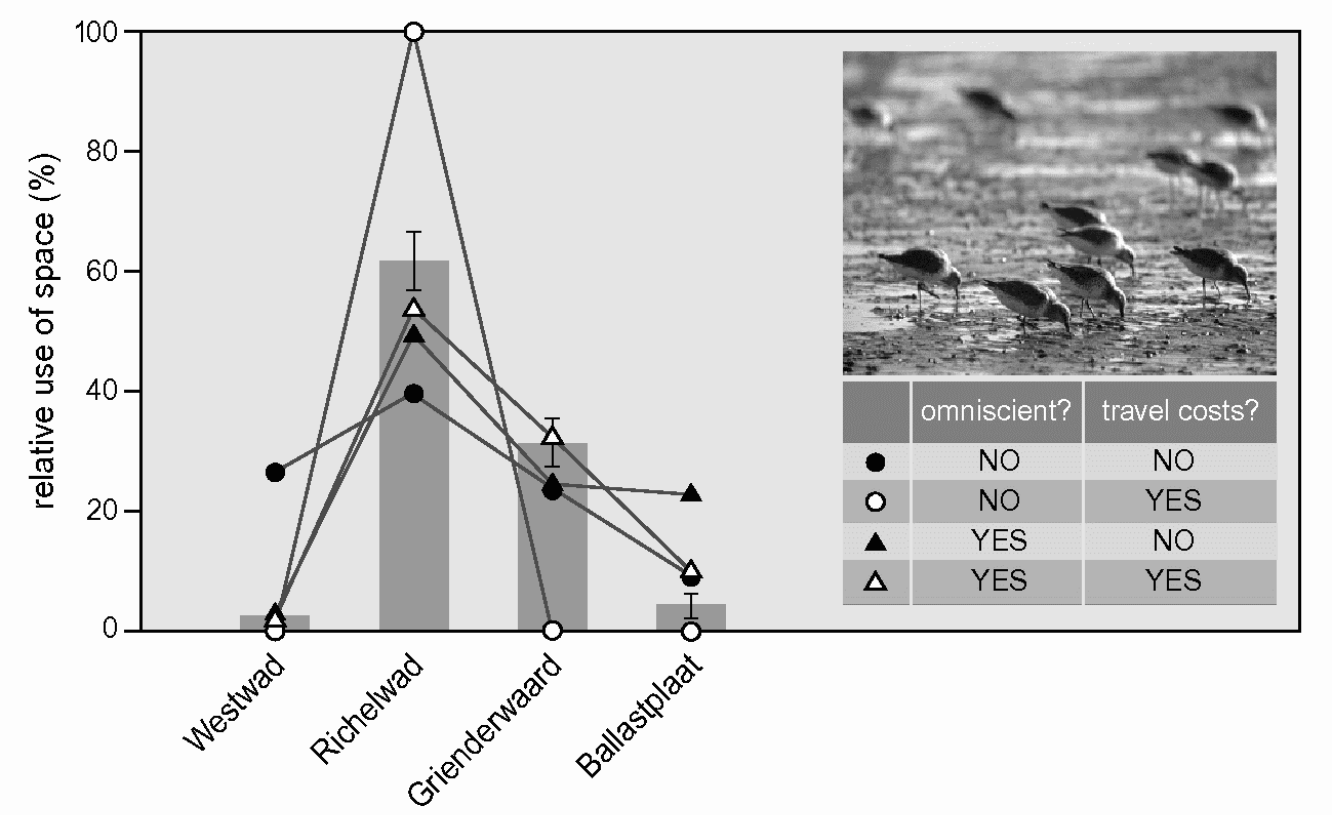

Figure 2. Relative distribution over the four intertidal feeding areas (see Fig. 1) of 121 Red Knots in the late summers of 1996-2000. These Red Knots were marked with small transmitters that were followed day and night with autmatic receiving station and manual radiotelemetry. For the present analysis, tidal cycles were selected during which birds spend the high water period at Richel. Based on van Gils *et al*. (2006).[8]

At the University of Groningen we have meanwhile started to examine disease prevalence and immune competence in tundra breeders and other bird species in earnest. One way of doing this is by the measurement of the capacity of small volumes of blood to kill certain bacteria and fungi *in vitro*.[14] This area of investigation recently received considerable support by the special fellowship from this university for Irene Tieleman. She will lead the development of a comprehensive research program on immune competence and disease in a variety of avian systems. We have high hopes that comparisons between species in different climate zones, and between seasons in the same birds, can yield greater insight into the roles of disease resistance and prevalence in decisions about habitat choice and in the regulation of numbers of animals.[15]

At this point it seems a good idea to say something about the *urgency* of our science. Right now the world is deeply concerned about avian influenza. All of a sudden our information on the distribution, the migration routes and the workings of the immune systems of waterbirds have become important.[16] Worldwide, animal ecologists try to help out with their data as much as possible. The large numbers of blood samples and cloacal swabs that have been accumulated from many different species and sites over the last few years now begin to have more than academic relevance. The results of our own involvement demonstrate that avian flu viruses are very rare in migrant shorebirds. The screening of many Great Knots *Calidris tenuirostris*, for example, a species that connects northern Asia via the Chinese coastal wetlands with Australia, has typically failed to find any viral infections.

The urgency of our work also stems from the concerns about the proper management of the world's last natural areas, about national and international policies with respect to complete protection of such areas or the admission of activities for short-term economic gains.[17] Our research on food, feeding and distribution of Red Knots in the western Dutch Wadden Sea has demonstrated that since 1988 the local stocks of the Baltic Tellin *Macoma balthica* has decreased by ninety-nine percent.[18] That is a drastic ecological change, as Baltic Tellins were one of they key species connecting the planktonic and epibenthic algal production with the wealth of migrant waterbirds for which the government of The Netherlands has claimed responsibility at international forums.

Baltic Tellins are not the only animals that have shown drastic population changes over the last thirty years. The sustained investigations by a whole army of un-, under-, or well-paid but always dedicated and knowledgeable ornithologists have led to incredible information on the changes in the avifauna of The Netherlands.[19] Since 1975 a few species have done very well. The Egyptian Goose *Alopochen aegyptiacus* that took our country by storm provides a good example. It is unfortunate that a much

greater number of species have disappeared from considerable parts of The Netherlands since 1975. The analyses made by SOVON have shown that species like Garganey *Anas querquedula*, Crested Lark *Galerida cristata* and Nightingale *Luscinia megarhynchos* have disappeared as breeding birds from much of the country. Even though the details of their disappearance have usually not been investigated, lack of food, an overabundance of predators, loss of breeding sites and the loss of connections with wintering areas are among the usual suspects of these declines. In most cases the hand of humankind is clear, although those in power usually prefer to attribute such losses and gains to things like climate change, i.e. causes that are outside governmental control!

A nice example of such a discussion is the variable interpretation of the causes of the extinctions of spectacular megafaunas that over the past 50,000 years have occurred in most parts of the world.[20] In the case of Eurasia, we lost animals such as the giant elk and the mammoth, as well as cave bears and cave lions. In the case of Australia, we lost a large array of large marsupials. Increasingly, the assembled evidence indicates that the rather comfortable explanation that these waves of extinction are due to climate change is no longer tenable. Temporal correlations between extinctions and bad ecological conditions are usually missing, whereas the correlations between extinctions and the arrival of modern man always occur.[20]

This is not to say that I believe that climate change plays no role as a causal agent of the distributional changes of animals. Rather to the contrary, it seems that considerable upheaval is underway.[21] Reflecting a rather continuous trend of loss of Artic ice, between 1979 and 2003 about one seventh of the ice cover of the North Pole region has disappeared, a loss of one million square kilometres of polar ice.[22] Climatologists have now also attempted to also make a *prediction* of the size of this icecap. The ice still covers much of the Arctic Ocean even in late summer, but by 2050, only 45 years from now, that surface may have been halved (Figure 3). This loss of ice cover will be something that today's young biologists will experience during their working lives. The loss of permanent ice cover will undoubtedly greatly influence the habitats in the Arctic and the animals that depend on those habitats.

Societal anxiety decides in a big way which areas of science will get additional financial support (the science of fear). It is thus very likely that climate change will

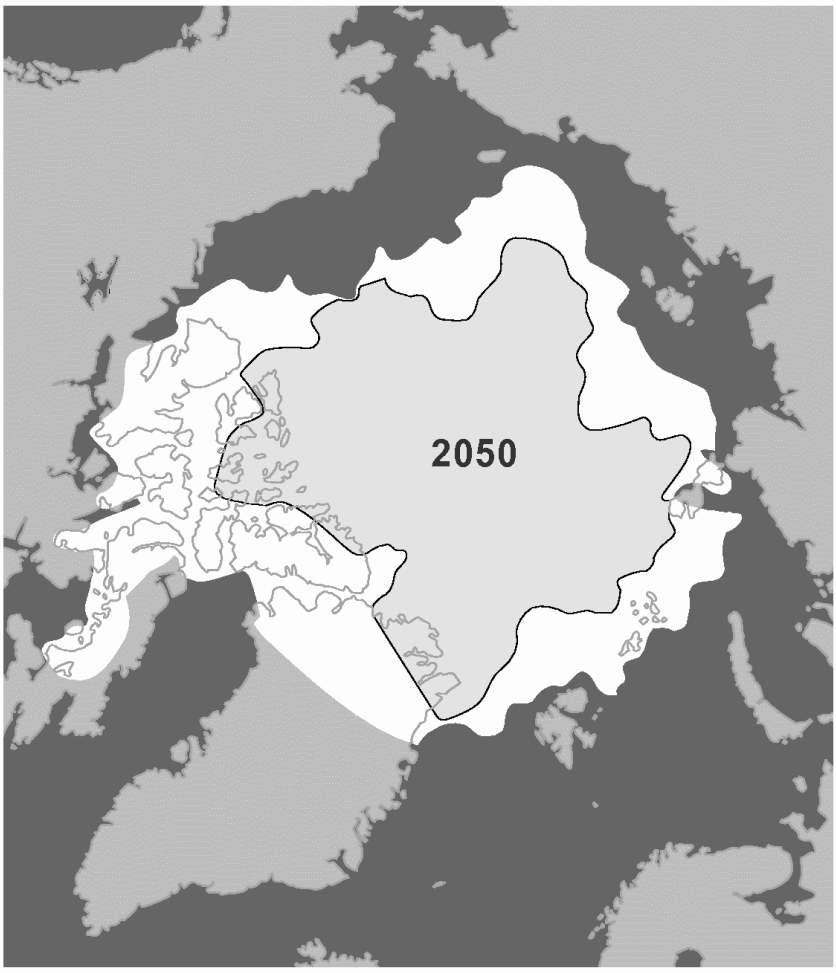

Figure 3. Predicted shrinkage of the North Polar icecap in late summer over the next fifty years from now. After Hamer (2006).[22]

increasingly determine the research agenda. Already, with a rise in global temperatures, an increasing number of studies report ecological change as a function of climatic change.[21] A nice example of such work is the Europe-wide analysis of the timing of breeding in Pied Flycatchers *Ficedula hypoleuca*. (At this point it is interesting to note that although the flycatcher work is 'hot' in the current climate of interest, it is built on many decades of purely scientifically motivated studies on flycatcher populations throughout Europe.) Based on a strong collaborative initiative together with the Netherlands Institute for Ecology (NIOO-KNAW) we are able to look back in time to see whether this species has adjusted to local climate change.[23] Bringing together long-term datasets from much of Europe, Christiaan Both and co-workers were able to demonstrate that Pied Flycatchers had started laying earlier only in localities where spring temperatures had increased. At places where spring temperatures had decreased, Pied Flycatchers had started breeding later in the season. In this quasi-experimental way it was demonstratede that changes in the timing of breeding are actually *caused by* climate change.

In the analyses of the timing of reproduction of Pied Flycatchers we look back in time. Often, however, we are asked to also make 'predictions'. In the case of the spring distribution and migration of Barnacle Geese *Branta leucopsis*, knowledge of causal mechanisms related to seasonal changes in food quality has become so advanced that geese researchers have now ventured to make such predictions.[24] In this particular example the predictions relate to changes in the seasonal phenology of food quality at different stopover sites along the flyway with a five degree increase in temperatures.

Urgency may be an important driving force behind patterns of funding, enjoyment and intellectual perspectives are crucial ingredients to get the best possible science! What gives our current animal ecologists their pleasure and perspective? Why is it a good (or at least an interesting) era to be an animal ecologist? In the first place I would like to mention the blossoming of ecological and evolutionary theory.[25] This is the process in which the consistency of verbal ideas are tested, and by which new and challenging questions are laid on the plate of the empirically minded.

The process can be illustrated by our recent work on distribution models of shorebirds. When animals are forced to forage in close proximity, they will be in each other's way and their intake rate will then go down. Figure 4 shows that at the best foraging patch, 'A' in this example, single animals achieve a high intake rate; as soon as more animals crowd together in A, their intake rate will decrease. When there are five animals in A, the sixth is better off in B. The twelfth animal better goes to the worst patch C. With increasing numbers the intake rate will go down for each of the animals. This so-called ideal free distribution model predicts that animals will achieve the same intake rates in all

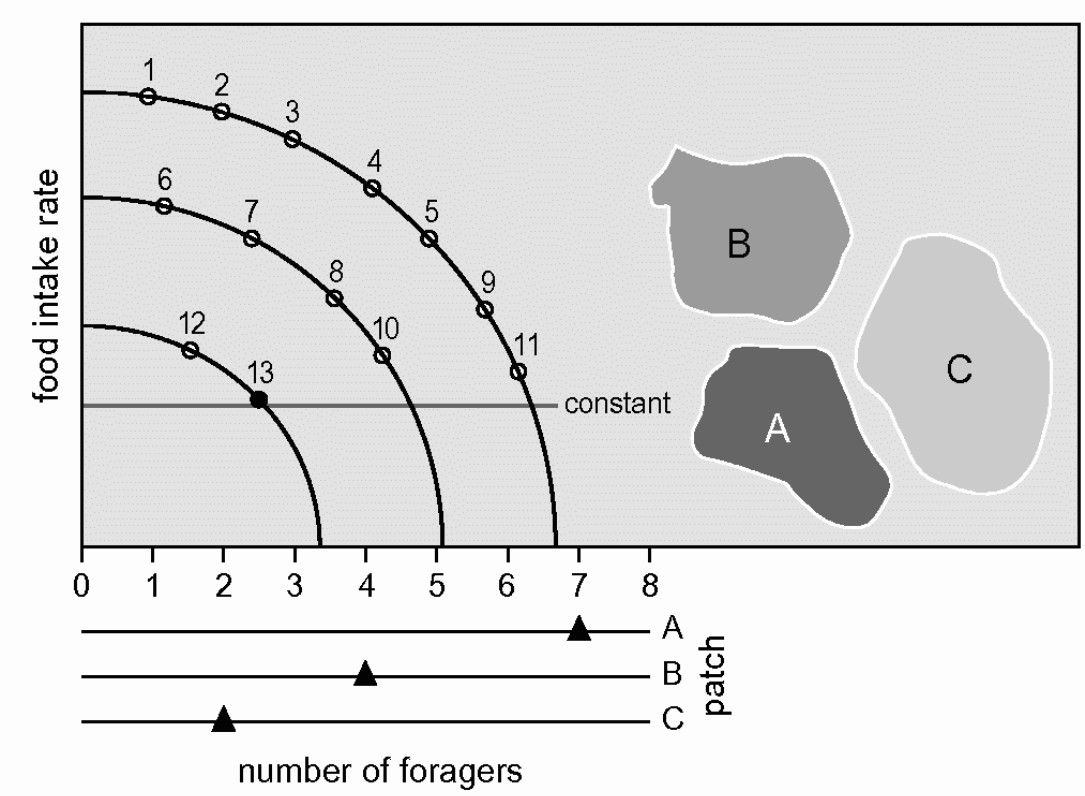

Figure 4. (Ideal free) model of the decrease in food intake rates with an increase in the density of foragers in three different patches (downcurved lines), A, B. and C, of decreasing quality. The numbered dots indicate how successive individuals choose the patch with the highest contemporary intake rate. The axes below the box give the final numbers of animals ending up in the different patches when a total of 13 animals has arrived.

patches.[26] By making shorebirds feed in different densities on small artificial mudflats in the Experimental Shorebird Facility at NIOZ, we try to test elements of such theories and also to evaluate what the consequences of increasing densities would be in field situations.[27] At this point we encounter a consideration of animals which I have failed to mention so far, their search for a balance between uncomplicated loneliness and living in pairs or groups, their SOCIAL MANAGEMENT.

Within our group ecological and evolutionary theories are tested at the scale of landscapes by Joost Tinbergen, Jan Komdeur and their co-workers. In this particular example they study the life history decisions of Great Tits *Parus major* in the Lauwersmeer area. They are interested in the extent to which the social environment affects fitness components (alternative behaviours such as clutch size or brood sex ratio) of individual animals. In this study the availability of multiple woodlots is used to advantage. In some lots the birds are manipulated to have small clutch sizes. This should reduce competition between offspring. To enhance competition in other woodlots clutch sizes are increased; in some the researchers increase the proportion of male fledglings, in others the proportion of female fledglings is increased. In this way the effects of sex ratio biases on survival and dispersion are experimentally evaluated.[28]

This is a great time to be an animal ecologist because genetic techniques to study subtle structures of relatedness within and between populations are now within reach.[29] We can go back even deeper in time to examine the effective population sizes and deeper layers of relatedness and past distributions. Co-operative ventures with relevant specialists also enable us to use the fast increasing spectrum of biomedical tools to examine body condition and health status of individual animals, and sometimes even to manipulate these variables in naturalistic contexts.[30]

Most of these methodological revolutions are made possible by intense international co-operation with animal ecologists and other specialists worldwide. The ease which we can communicate over the internet is very helpful in this context, and of course relatively cheap international air travel helps as well.

As an example of the new power of insightful comparisons on a worldwide scale is the comparative demographic work on migrant shorebirds in which we take the lead. This map (Figure 5) shows the global flyway network spun by the migratory routes of Red Knots, Red Knots that fan out to all coastal corners of the world from their circumpolar tundra breeding grounds. To achieve an understanding of the evolution and maintenance of the migration systems, with a sense of urgency because of the worldwide threats to the coastal ecosystems on which they depend, long-term demographic studies are now underway for five of the six subspecies. By marking individuals with unique combinations of colour bands and leg flags that are easy to read in the field, and by making sure that sufficient efforts are made to continue reading these colour

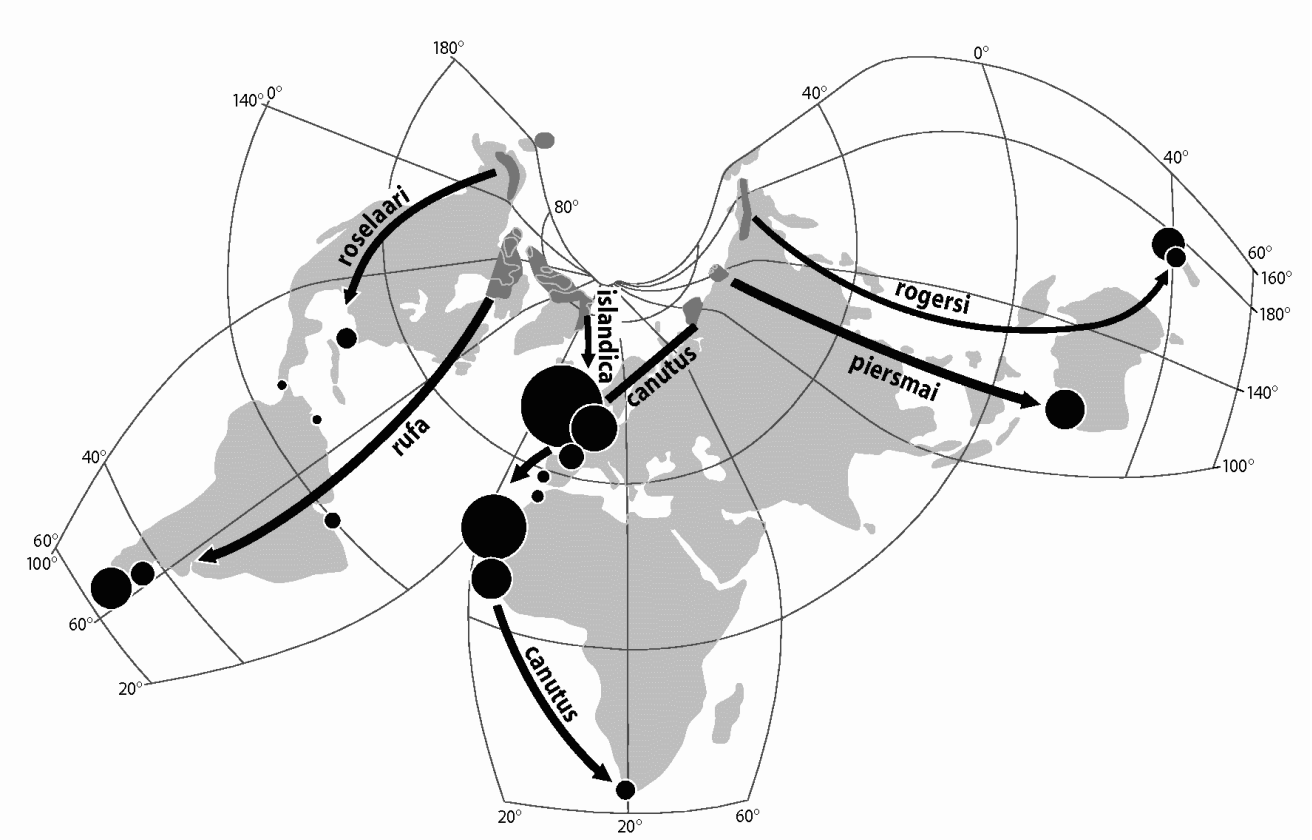

Figure 5. The worldwide network of flyways of the six subspecies of Red Knot. The dots scale to the approximate size (in 2004) of the respective wintering populations. In all subspecies except *roselaari* intense and focused demographic studies are underway.

combinations, we are now in the position to examine many individual itineraries and to get robust year-by-year estimates of annual survival. Comparisons between subspecies will be very instructive, as will be comparisons between closely related shorebird species.[31] In the meantime demographic research projects are also in hand for four of the five subspecies of Bar-tailed Godwits *Limosa lapponica*.

In this context I am very pleased to announce the moral and financial support that we are starting to receive for this worldwide flyway research[32] by Vogelbescherming-Nederland, the Dutch branch of the BirdLife International partnership. Vogelbescherming has reached the conclusion that the protection of birds needs to be based on solid scientific evidence, and have demonstrated this by supporting new work on the annual cycles of Montagu's Harriers *Circus pygargus* and Skylarks *Alauda arvensis*.

The power of intensive colour-marking projects and other kinds of co-operation can further be illustrated by our new studies on the stopover ecology and migrations of the Ruff *Philomachus pugnax*. It is fantastic to be able to collaborate in this project with the passionate specialist amateur bird catchers and ringers known as 'wilsternetters'.[33] Wilsternetting is an old craft by which the netters try to attract flocks of Eurasian Golden Plovers *Pluvialis apricaria* or Ruffs to a netting site with strong audiovisual stimuli. Upon arrival the birds are caught in midair by the huge net that is pulled up in front of them. Thanks to the wilsternetters we were able to individually colour-mark as many as 2400 ruffs during the past two spring seasons. Observers over much of Europe and in West Africa ensured that within a short period of time we have already built up quite a comprehensive picture of the flyway of Ruffs staging in the west of the province of Fryslân (Figure 6). That this has been achieved within two years of study, also means that we should be able to document changes in flyways in real time; these changes may be a consequence of habitat loss, habitat modification, or climate change.

It is a good time to be an animal ecologist because of fast technological developments, especially with respect to the miniaturization and user-friendliness of all kinds of gadgets. Satellite transmitters are now so small that they can be implanted within the belly cavity of the large female Bar-tailed Godwits breeding in Alaska. The implantations are a veterinary masterpiece, and animals mounted with these new devices survived the applications and explored the shores of the Bering Sea in preparation of the 11,000 km long flight across the whole Pacific toward the wintering grounds in New Zealand. In 2006 Bob Gill and his team were successful in obtaining tracks of birds overflying the Pacific.[34] Although the technology still needs improvement, the dream of following individual small birds across much of the globe is within reach. In Groningen we have meanwhile also been involved in some successful satellite tracking studies on bigger birds such as Brent Geese *Branta bernicla* and Barnacle Geese.[35] On the down side, we all know about the tragic fate of one of the two female Montagu's Harriers that were fitted with satellite tags on their breeding ground in the east of the province of Groningen. As could be read in the newspapers, the harrier called Marion travelled all the way from Groningen to northern Nigeria where she was killed by the hand of man.[36]

Most bird species are much smaller than Bar-tailed Godwits and Montagu's Harriers, and new developments in migration ecology have certainly been hampered by the unavailability of truly small transmitters. We are now engaged in a co-operative venture with Cornell University to develop really small gadgets that combine sensors and a capacity for data storage with the ability to transmit these data at certain - predetermined - points in time. The only thing we have to do is to apply the transmitters and then be there to listen for them a year later.

We hope to begin employ these transmitters in new research on the details of the migration of Red Knots that spend the winter on the intertidal mudflats of Banc d'Arguin, that incredibly important and famous wetland in coastal Mauritania. Here we have already found strong local differences in the annual survival of birds that are faithful to roosts and feeding areas west and east of the village of Iwik.[37] Birds that have their home range west of Iwik have an annual survival of approximately 76% whereas birds that only occur east of Iwik have an annual survival of only 56%. We suspect that the 20% difference in annual survival reflects differences in the quality of the respective mudflat feeding areas (but are puzzled by the factors leading to the maintenance of such striking differences). Whatever the reasons for the survival difference, it provides us with a great contrast in wintering conditions that may enable us to investigate how quality differences between wintering habitats have downstream effects later in the year. Using the archival tags we hope to detect the seasons and sites where the differences in annual survival originate and to learn whether they are related to events during migration on the French or German spring stopover sites.

I must conclude that our enterprise is in full swing. I hope that I have made clear that animal ecologists like us begin to come to grips with all factors that influence habitat choice and animal numbers. We have an increasing spectrum of technical means at our fingertips to study all these factors in an integrative way in several major ecosystems. The strength of our animal ecology, the combination of theoretically inspired large-scale fieldwork with the experimental testing of the theories themselves, forms the basis of a worldwide web of inspiring collaborations.

At this point I am close to the end of this lecture. It is time for another citation, a citation with which Koos van Zomeren began his series of public lectures at this university: "*Well aware of his impermanence, man searches for a relationship with that which is permanent, the eternal, that which will certainly survive. This can be a God. This can be children. This can be art. This can also be the landscape… but not if this landscape is more impermanent than us*."

I would suggest that it could also be *science*, but only science of the inspiring, elegant and 'timeless' kind. When I started off as a university professor two and a half years ago, I hoped to find that within the walls of this 400 year old university the fight for fragile scientific enterprise would be self-evident. I was somewhat dismayed to discover that such an attitude can *not* be taken for granted. Nevertheless, I

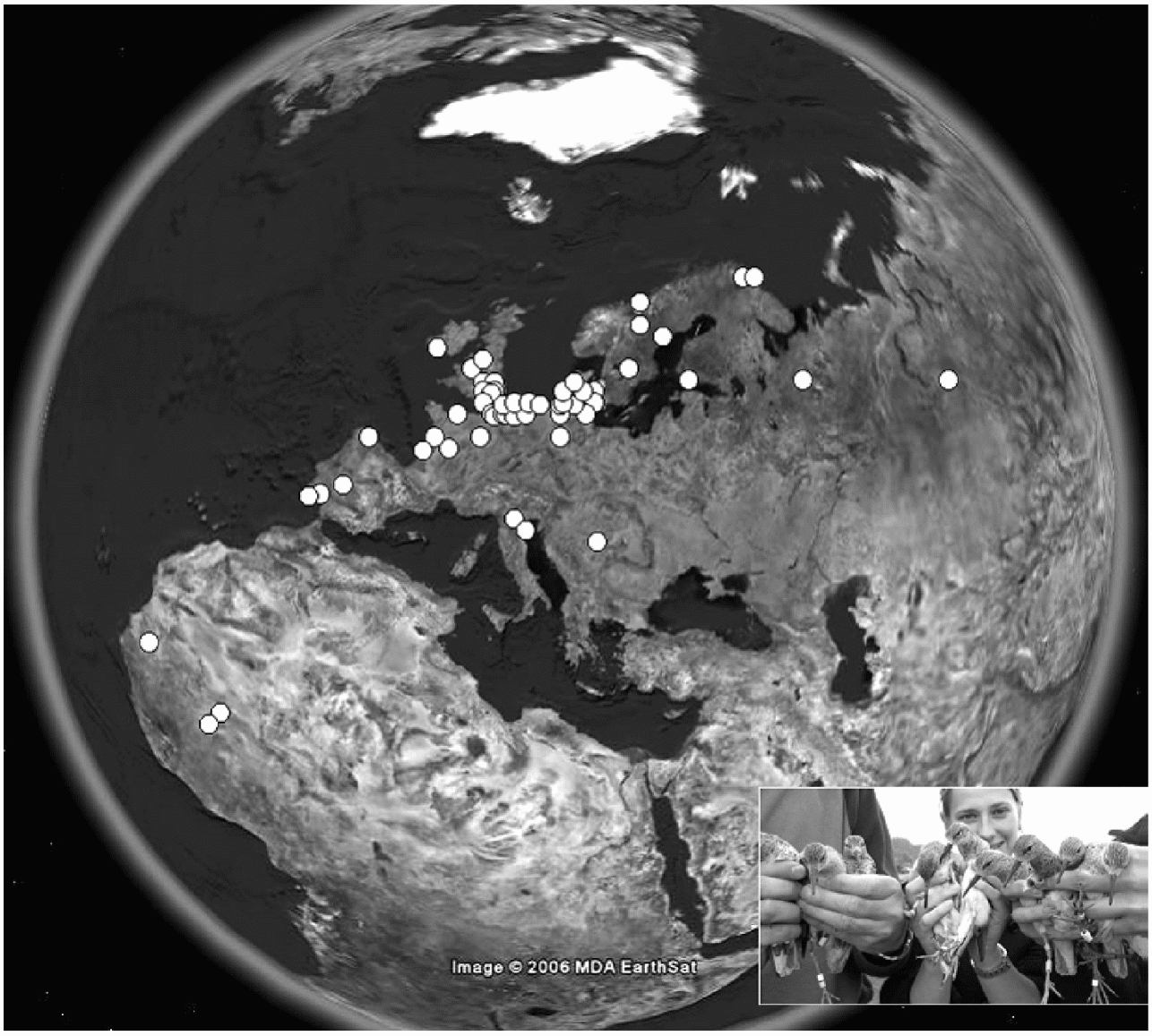

Figure 6. Locations of recovery or resighting (complete till December 2005) yielded by the 2400 Ruffs that were captured by the Friesian wilsternetters in the springs of 2004 and 2005 in southwest Fryslân and provided by the RUG-team with individual colour-ring combinations.

remain hopeful that at this university, and at our fundamental research institutions as well, we will find ways to try and avoid the treacherous temptation of the 'market'. I believe that succumbing to market forces inescapably leads to the loss much of what is good about our scientific legacy. Only recently, Piet Borst in his column for a national Dutch newspaper (NRC Handelsblad)[38] stated the following: "*All this thematically funded research pushes scientists to run from one money-tap to another to fill their buckets. This selects for handymen, not for brilliant innovators. The fixation on trendy subjects and sexy research priorities also narrows down the basis [of our work]…*". In the case of contract-research, the customer will eventually be king. This is not necessarily a problem if both parties share the need for new hard knowledge. In ecology, however, this is rarely the case. In such instances the soundness and freedom of science is at stake. As much as we need autonomous courts of justice, just as much civil society needs autonomous science.[39] Thus, we need to stand in defence of the Ivory Tower; an ivory tower, of course, with wide open windows through which beautiful and important new knowledge will radiate.

ACKNOWLEDGEMENTS

I thank Ken Rogers for suggesting this essay might be a fitting contribution to the celebratory issue of *The Stilt*, and for help in producing it. In my lecture I thank many close friends and colleagues from The Netherlands, but the scope of the enterprise is obviously international. In fact, I cannot really find the proper words to describe what it means to me to be part of that worldwide network of dear friends and colleagues. For starters, I can't get enough of the committee and the membership of the International Wader Study

Group! In addition, and in particular, I extend my warmest thanks for being there to Allan Baker, Patricia Gonzalez, Grant Pearson, Hugh Boyd, Phil Battley, Danny and Ken Rogers, Bob Gill and Colleen Handel, Åke Lindström, David Winkler, Pavel Tomkovich, Yaa Ntiamoa-Baidu, Chris Hassell and others. Our intense communications are so exciting and our occasional get togethers and joint adventures so incredibly cool. I thank Dick Visser for his usual patience and eye for detail in making and editing the illustrations.

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